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ʻŌhiʻa Dieback in Hawaiʻi: Vegetation Changes in Permanent Plots[1]

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ABSTRACT: Approximately 50,000 ha of native ʻōhiʻa (*Metrosideros polymorpha* Gaud.) forest on the island of Hawaiʻi experienced a drastic reduction (dieback) of the tree canopy between 1954 and 1977. Concern for the management of this important native ecosystem has stimulated a great deal of research on the Hawaiian dieback phenomenon. In this paper we address the question of changes in the ʻōhiʻa population after an area has experienced dieback.

Since 1976, we have established 62 400-m^2 vegetation sampling plots throughout the dieback and adjacent nondieback forest areas on the island of Hawaiʻi. The tall tree vigor and ʻōhiʻa seedling and sapling growth were resampled in 26 of these study plots in 1982. The results of the reassessment of the ʻōhiʻa populations indicate that the forest dieback has not spread appreciably since 1977. However, nearly all the plots located in areas that originally experienced a drastic reduction of the tree canopy cover were found to have a large number of ʻōhiʻa seedlings and saplings. Based on this apparent high level of regeneration following the initial canopy loss, we speculate that most of the forest dieback areas will again develop a closed, tall-statured ʻōhiʻa tree canopy.

ʻŌHIʻA DIEBACK AND ʻŌHIʻA FOREST DECLINE are terms that came into common use in Hawaiʻi during the early 1970s to describe the widespread death or defoliation of ʻōhiʻa (*Metrosideros polymorpha* Gaud., Myrtaceae), the dominant, canopy-forming tree species in much of the native Hawaiian forest (Burgan and Nelson 1972; Mueller-Dombois 1980; Mueller-Dombois, this issue). The earliest mention of this phenomenon was nearly 75 years ago when an area of wet forest on the eastern portion of the island of Maui experienced a similar dieback (Lyon 1909). In recent years, ʻōhiʻa dieback has been reported from several of the major Hawaiian islands, but has reached its greatest extent and intensity in the wet, windward forests on the island of Hawaiʻi (Jacobi 1983; Mueller-Dombois et al. 1980; USDA Forest Service 1981).

Petteys, Burgan, and Nelson (1975) discussed the spread of the "epidemic decline" in an 80,000-ha study area on the island of Hawaiʻi, from an analysis of aerial photographs taken in 1954, 1965, and 1972. They described an increase in what they called "severe ʻōhiʻa decline forest" from 120 ha in 1954, to 34,500 ha in 1972. In a more recent assessment, Jacobi (1983) found that approximately 50,000 ha of this ʻōhiʻa forest was in dieback ($>50\%$ of the canopy trees dead or defoliated) by 1977. Petteys et al. (1975:11) concluded, "if decline continues at the present rate, remaining ʻōhiʻa forest in the study area will be virtually eliminated in 15 to 25 years."

Concern for the management of this native ecosystem, which is both an important watershed and a habitat for numerous species of endangered plants and animals, has stimulated a great deal of research on the Hawaiian dieback phenomenon. The focus of this work has been to better understand both the mechanism and consequences of ʻōhiʻa dieback (Mueller-Dombois, this issue; Mueller-Dombois et al. 1980; USDA Forest Service

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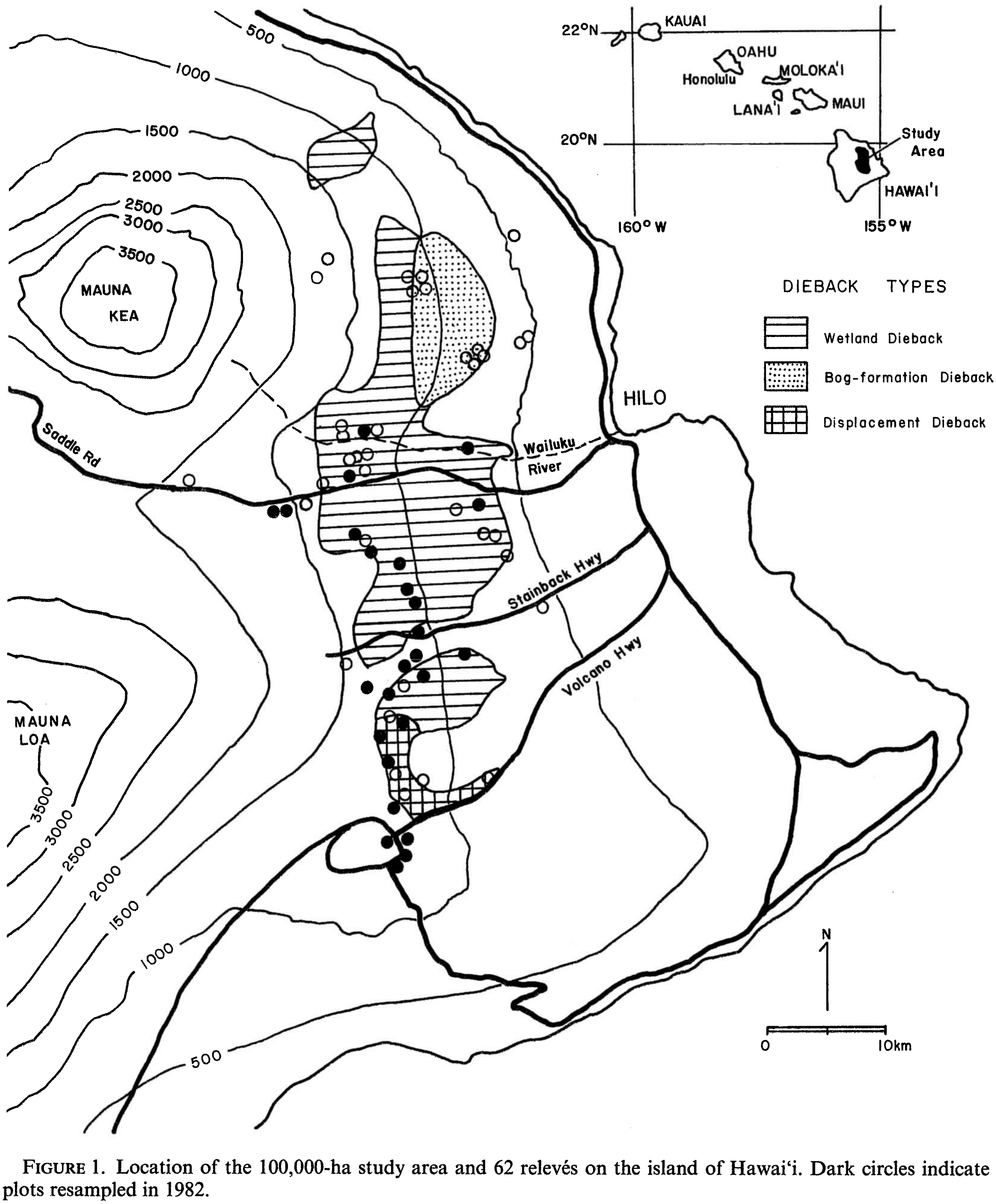

FIGURE 1. Location of the 100,000-ha study area and 62 relevés on the island of Hawai'i. Dark circles indicate plots resampled in 1982.

1981). In the present paper we address the latter point, with an assessment of changes in the ʻōhiʻa population over time, from a series of study plots established across the major area of forest dieback on the island of Hawaiʻi.

METHODS

Field Sampling

Since 1976 we have established 62 20 × 20 m study plots (relevés) throughout a

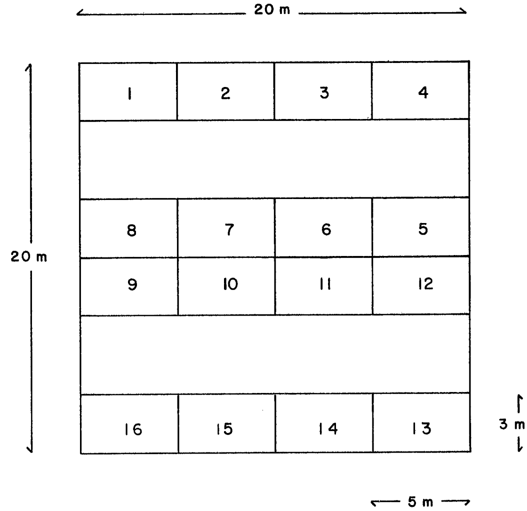

FIGURE 2. Sampling design within the 20 × 20 m relevés.

100,000-ha study area on the windward side of the island of Hawai'i (Figure 1). In each relevé, data were collected on both the composition and structure of the vegetation and on basic characteristics of the substrate (Mueller-Dombois et al. 1980).

Foliage cover was estimated for all species of plants using the Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). Additionally, the total number of individuals of both *Metrosideros* seedlings (defined as 0.1–0.5 m tall) and saplings in five stem-height classes (0.5–1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m tall) were counted in a series of 3 × 5 m subplots established systematically within each relevé (Figure 2). Finally, we recorded diameter at breast height (DBH) and vigor for all trees greater than 5 m tall in the plot. Relevés that contained less than 30 trees were expanded to attain at least this minimum number. All measured trees were also permanently marked so they could be reassessed in the future.

Tree vigor was recognized in five classes based on the degree of crown defoliation for live trees and the relative age of dead trees, following the classification developed by Mueller-Dombois et al. (1980). Individual tree vigor classes were defined as follows:

CLASS 1: Trees with fully foliated crowns.

TABLE 1

DESCRIPTION OF THE FIVE FOREST VIGOR CLASSES, BASED ON THE DIEBACK INDEX CALCULATED FOR EACH RELEVÉ

DIEBACK INDEX (%)	FOREST VIGOR CLASS	DESCRIPTION
0.0–10.0	1	No dieback
>10.0–25.0	2	Slight stand dieback
>25.0–50.0	3	Moderate dieback
>50.0–75.0	4	Heavy dieback
>75.0	5	Severe dieback

CLASS 2: Trees with some defoliated branches; <50% of the crown dead.

CLASS 3: Trees with most of the upper crown branches defoliated, but with abundant epicormic branching along the trunk.

CLASS 4: Relatively recently dead trees with some fine branches (<5-cm diameter) and most of the bark remaining.

CLASS 5: Old, dead trees with only major branches remaining and most of the trunk without bark.

Tree vigor classes 1 and 2 were considered to constitute the "healthy" tree group in our analyses, despite the loss of some of the crown in class 2 trees. Classes 3–5 made up the "nonhealthy," or dieback, tree group. The percentage of trees in the nonhealthy group was termed the Dieback Index for each relevé. This Dieback Index allowed the plot to be assigned to one of five forest vigor classes (Table 1). In this classification, stands that had only a few trees (<25%) in the dieback tree group were considered to be in the no-dieback or slight-dieback categories. Stands with >50% dieback were considered to be in heavy- or severe-dieback categories.

Reassessment of Selected Relevés in 1982

Twenty-six of the relevés that had been established in 1976–1977 (hereafter referred to as 1977) were resampled in 1982 to assess changes in both canopy tree vigor and 'ōhi'a regeneration over that 5-yr period (Figure 1). These samples included relevés located in forests in all stages of stand vigor, from non-dieback stands (Dieback Index $<10\%$), to stands with most of the tall trees dead or defoliated (severe dieback). The dieback stands represented four of the five dieback types originally described by Mueller-Dombois et al. (1980) and Mueller-Dombois (this issue). These types included "wetland," "dryland," "displacement," and "hot-spot" dieback (see Jacobi 1983). Hot-spot dieback, as used in this context, is a structural category that refers to small patches of dead trees found in densely stocked stands.

In the 1982 reassessment, data were collected on tree vigor for all marked trees within each relevé; and all seedlings and saplings found within each of the 16 subplots were counted. For the saplings, an additional height class was recognized (>5 m tall) to accommodate individuals that had grown beyond the limits of the 4–5-m height class since the initial survey.

RESULTS AND DISCUSSION

The results of the initial sampling and reassessment of the 26 relevés are summarized in Table 2, where the relevés have been separated into six groups (A–F) based on dieback type and dieback intensity. The two plots in the hot-spot dieback category (A) showed heavy to severe dieback for both sampling times. The three relevés in forests classified as displacement dieback (B) had less than 50% of the canopy trees dead or defoliated both times. Finally, the dryland and wetland dieback types sampled had several relevés in both slight-to-moderate and heavy-to-severe dieback condition.

Tree stocking was found to be variable across the set of sample plots. No clear relationship could be found between the number of trees per hectare on a particular site and the dieback type or intensity. The stands with particularly high tree-stocking values (relevés 13, 14, 30, and 35) represented early seral stages of vegetation that had developed on relatively young volcanic lava or cinder substrate.

Changes in Canopy Tree Vigor from 1977 to 1982

In our reassessment of the 26 relevés throughout this forest, the ten plots classified as being in slight to moderate dieback (less than 50% of the canopy trees dead or defoliated) did not show a marked increase in dieback intensity when resampled in 1982. This trend is in contrast to the rapid increase in the aerial extent of severe canopy loss in this windward forest, which was identified by Petteys et al. (1975) for a similar period of time between 1965 and 1972. Our results are consistent with recent observations that the dieback event in this forest was generally confined to the period starting in the early 1960s and ending in the mid-1970s (Jacobi 1983).

Assessment of ʻŌhiʻa Regeneration Potential

Previous investigations have shown that although ʻōhiʻa seeds are quite abundant in most forest stands, the developing saplings are not able to tolerate the low light conditions typically found below the closed tree or tree fern (*Cibotium* spp.) canopy (Burton 1980, Cooray, in preparation, Mueller-Dombois et al. 1980). Therefore, until the canopy is opened up, ʻōhiʻa forests typically have a relatively small number of saplings. Most of these immature individuals are found growing as epiphytes in positions with more light, such as on tree fern trunks, or in crotches of the larger trees (Burton 1980, Rock 1917).

The replacement of mature trees in a stand is a function of the establishment and subsequent successful growth of immature individuals over time. In the case of ʻōhiʻa forests, the shade-intolerant characteristics of this species preclude a steady-state population structure, as is typical of climax communities (Whittaker 1975). The maintenance of ʻōhiʻa as the dominant species must be accomplished either through the occasional opening of the canopy by, for example, windthrown trees, or by a more widespread canopy disturbance, such as results from dieback. However, Petteys et al. (1975:3) reported that "the [dieback] epidemic is affecting all

TABLE 2

SUMMARY OF FOREST VIGOR AND 'ŌHI'A POPULATION IN THE 26 RELEVÉS REASSESSED IN 1982

GROUP	RELEVÉ	DIEBACK TYPE (INTENSITY)	DIEBACK INDEX (%) 1977	DIEBACK INDEX (%) 1982	TREES/HA	SEEDLINGS/HA 1977	SEEDLINGS/HA 1982	SAPLINGS/HA 1977	SAPLINGS/HA 1982	SAPLINGS: TREES 1977	SAPLINGS: TREES 1982
A	13	Hot-spot (heavy)	73.2	Not calc.	3,550	833	1,666	333	499	0.1	0.1
	37	Hot-spot (severe)	92.8	100.0	350	17,374	2,208	374	249	1.0	0.7
B	22	Displacement (none–slight)	0.0	27.2	275	83	499	0	124	0.0	0.4
	32	Displacement (moderate)	20.0	45.0	242	166	2,374	0	0	0.0	0.0
	29	Displacement (moderate)	33.3	46.6	375	124	708	0	0	0.0	0.0
C	14	Dryland (slight)	11.2	21.6	1,550	249	0	708	458	0.4	0.3
	30	Dryland (slight–moderate)	19.4	30.9	1,800	8,208	4,541	1,374	1,583	0.8	0.9
D	20	Dryland (heavy)	61.1	66.6	900	4,791	1,958	458	874	0.5	0.9
	26	Dryland (heavy–severe)	91.6	70.0	600	21,874	8,291	1,458	1,666	2.4	2.8
	18	Dryland (severe)	100.0	92.8	700	5,666	3,874	1,749	3,999	2.5	5.7
E	35	Wetland (slight–moderate)	29.8	21.0	1,425	833	249	499	83	0.3	0.1
	23	Wetland (slight–moderate)	18.1	35.4	825	2,083	499	0	0	0.0	0.0
	33	Wetland (slight–moderate)	25.8	41.9	775	291	166	0	0	0.0	0.0
	27	Wetland (slight–moderate)	29.4	12.1	850	5,833	3,916	166	666	0.2	0.8
	25	Wetland (moderate)	35.7	33.3	450	333	666	4,499	8,083	10.0	18.0
F	43	Wetland (heavy)	58.0	53.5	775	10,083	9,249	416	1,749	0.5	2.3
	38	Wetland (severe)	83.3	83.3	176	3,624	7,166	249	458	1.4	2.6
	34	Wetland (severe)	87.8	79.3	825	25,499	16,749	1,333	2,749	1.6	3.3
	24	Wetland (severe)	85.7	90.4	525	12,124	9,249	749	2,041	1.4	3.9
	19	Wetland (heavy)	50.0	65.0	500	2,416	416	2,166	2,499	4.3	5.0
	11	Wetland (severe)	94.5	Not calc.	925	13,416	2,999	5,416	5,249	5.9	5.7
	28	Wetland (severe)	88.2	80.0	412	6,916	1,499	2,833	2,458	6.9	6.0
	12	Wetland (severe)	100.0	100.0	750	20,499	6,666	2,499	5,249	3.3	7.0
	42	Wetland (severe)	84.2	89.4	475	16,249	9,416	1,208	3,749	2.5	7.9
	15	Wetland (severe)	92.8	91.6	433	24,749	8,458	4,583	8,666	10.6	20.0
	39	Wetland (heavy–severe)	71.4	83.3	221	3,666	1,041	3,291	4,916	14.9	22.2

NOTE: Seedlings, 0.1–0.5 m tall; saplings, 0.5–5 m tall; trees, >5 m tall.

ages of trees on widely different sites." This being the case, it would be expected that following dieback, both the structure and composition of this forest would be permanently changed.

In our study, 'ōhi'a regeneration potential was assessed by examining the number of trees (>5 m tall), seedlings (0.1–0.5 m tall), and saplings (0.5–5 m tall) per hectare for each of the 26 relevés. A basic assumption in this analysis is that the height classes defined for individuals less than 5 m tall are correlated with age. Unfortunately, there has been no success in recent attempts to determine ages of 'ōhi'a trees using standard dating techniques (K. Adee, personal communication; J. P. Lockwood, personal communication).

'Ōhi'a Seedling Abundance

The number of seedlings per hectare was found to vary considerably among the stands sampled, and between the first and second sampling periods. It can generally be said that most of the relevés in heavy to severe dieback had an extremely large number of seedlings per hectare when sampled. An exception to this observation is one of the hot-spot dieback stands (relevé 13) which, even in 1982, had less than half the number of seedlings as mature trees, despite severe crown defoliation prior to 1977.

All the relevés in the displacement dieback group (B) showed an increase in seedling density in 1982. With the exception of relevés 13, 25, and 38, all the other stands showed a decrease in the number of seedlings per hectare, regardless of dieback type or intensity.

We hesitate to speculate much on the significance of these changes in seedling density in the context of regeneration of 'ōhi'a following canopy dieback. It is likely that the variation in seedling density detected in the samples is more a result of a phenological cycle rather than a successional trend.

'Ōhi'a Sapling Abundance

The number of saplings (0.5–5 m tall) per hectare appears to be a more reliable indicator of regeneration potential for the 'ōhi'a stands sampled. By focusing on these presumably older individuals, we can hopefully eliminate seasonal variations that may influence the abundance of seedlings in a particular site.

A rough index of regeneration potential in a given stand was obtained by calculating the ratio of the total number of saplings per hectare (all height classes combined) to the number of tall trees per hectare. This index is based on the premise that the regeneration of stands affected by canopy tree dieback can be considered successful if each of the dead or dying trees is eventually replaced by a new healthy tree.

When this ratio is examined for the six groups of relevés in Table 2, some relationships between dieback type and intensity with regeneration potential become evident. With the exception of relevé 25, none of the stands in slight-to-moderate dieback condition (groups B, C, and E) had a ratio of saplings to trees greater than 1. In contrast, all the heavy-to-severe dieback stands, except for the hot-spot stands (group A), had a ratio of at least 1, with most of them showing a ratio of greater than 3:1 by 1982. Additionally, most of the dieback plots showed an increase in the ratio of the number of saplings to trees when they were sampled the second time.

Structural Analysis of the 'Ōhi'a Populations Sampled

Frequency plots of the sapling data are shown in Figures 3–6. These histograms display the number of individuals per hectare in each height class for the two sampling dates. Additionally, the number of mature trees per hectare is indicated on the graphs by a solid, horizontal line. The histograms are separated into four groups, based on the relative abundance of saplings (as compared to canopy tree stocking) in the different height classes. For the present discussion these groups are identified as (1) no apparent regeneration (Figure 3); (2) early regeneration (Figure 4); (3) advanced regeneration (Figure 5); and (4) very advanced regeneration (Figure 6).

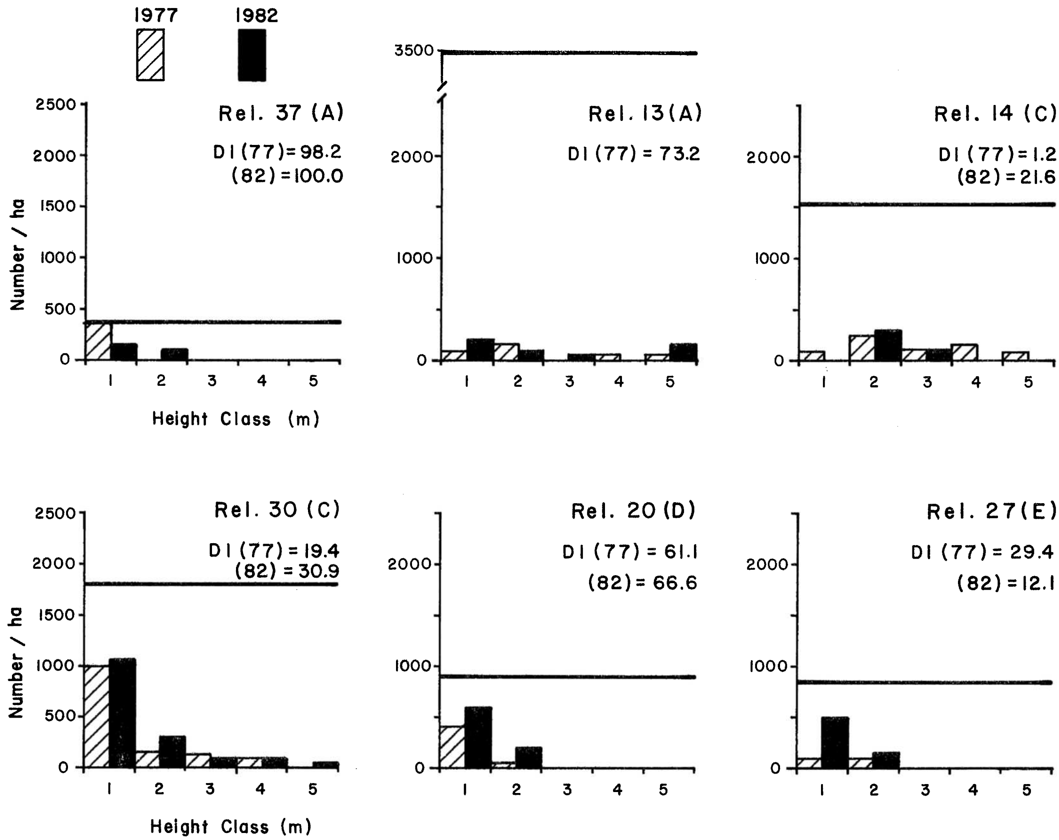

FIGURE 3. Frequency histogram of the number of saplings (0.5–5 m tall) per hectare for the different height classes recognized—"no regeneration" group. The number of mature trees per hectare is indicated by the solid, horizontal line on each graph.

The first group (Figure 3) actually includes several other relevés (22, 23, 29, 32, 33, and 35) for which relatively few, or no, saplings were recorded. Although some of the stands included in this first group had a small number of saplings in the 4–5-m height class, all those relevés had a total sapling-to-tree ratio less than 1 for at least 1982. Additionally, all the relevés in this group, except 20, 13, and 37, were located in stands with a Dieback Index less than 50%.

The second group of graphs (Figure 4) includes five relevés with a relatively large number of saplings in height class 1 (0.5–1 m), but few or no individuals in the larger classes. All these stands were classified as being in heavy to severe dieback in both 1977 and 1982.

Groups 3 and 4 (Figures 5 and 6) are composed of stands with an even greater number of saplings in the larger height classes. At least for 1982, the six relevés in group 4 show a departure from the "inverse-J-shaped," or negative exponential, curve seen in the plots for groups 2 and 3. Instead, the histograms in group 4 approach a more normal shape, resulting from a smaller number of individuals in the 0.5–1-m height class, as compared to the next larger class. Except for relevé 25, all the stands in groups 3 and 4 have a Dieback Index greater than 50% for both 1977 and 1982.

'Ōhi'a Regeneration Patterns in Relation to Canopy Dieback

There appears to be a strong relationship between the degree of canopy dieback in a

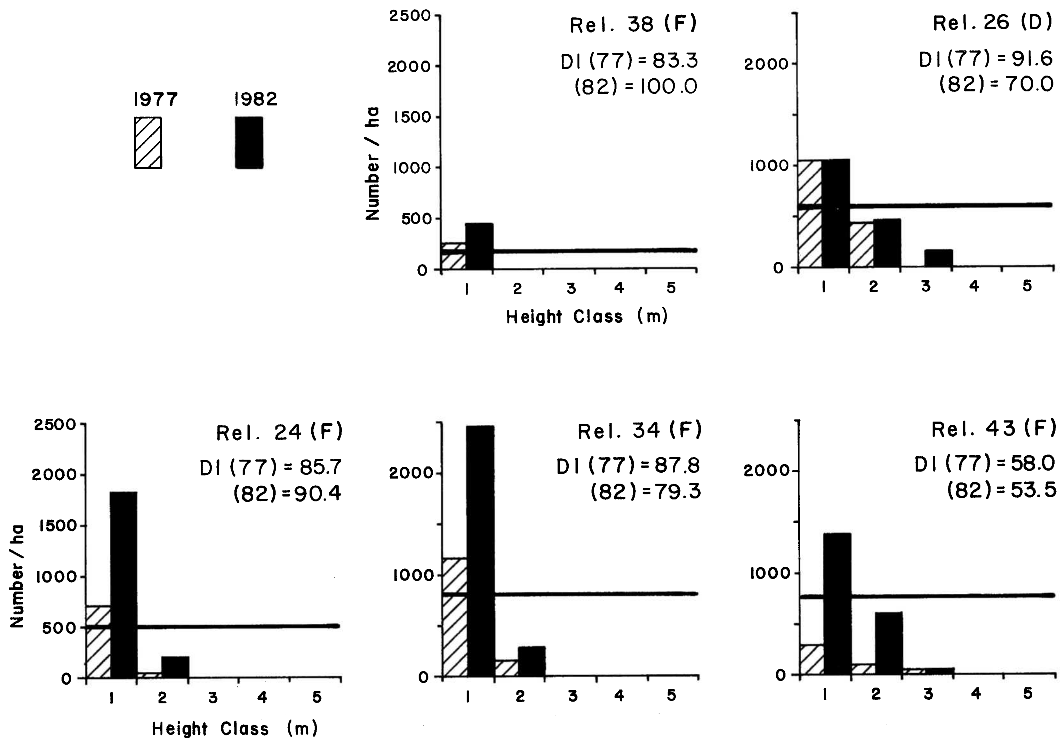

FIGURE 4. Frequency histogram of the number of saplings (0.5–5 m tall) per hectare for the different height classes recognized—"early regeneration" group. The number of mature trees per hectare is indicated by the solid, horizontal line on each graph.

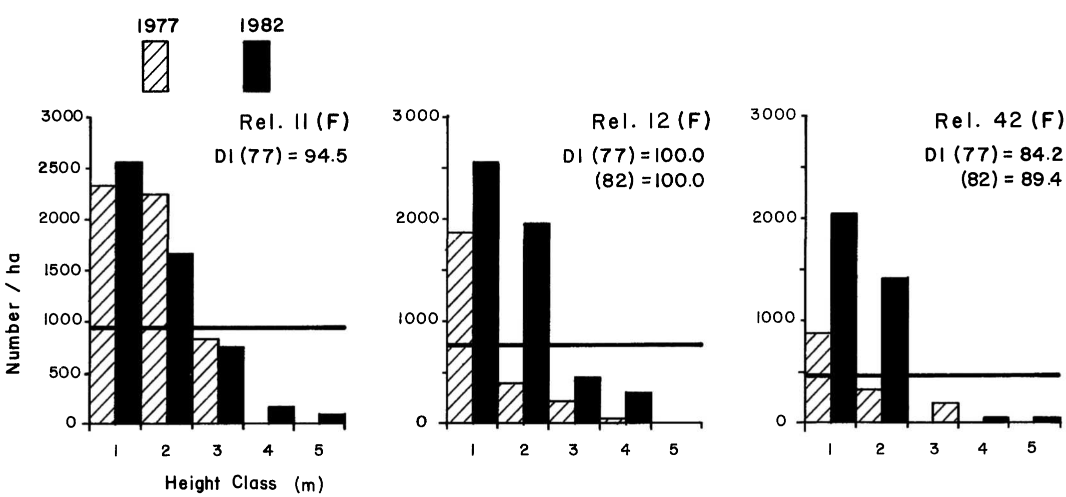

FIGURE 5. Frequency histogram of the number of saplings (0.5–5 m tall) per hectare for the different height classes recognized—"advanced regeneration" group. The number of mature trees per hectare is indicated by the solid, horizontal line on each graph.

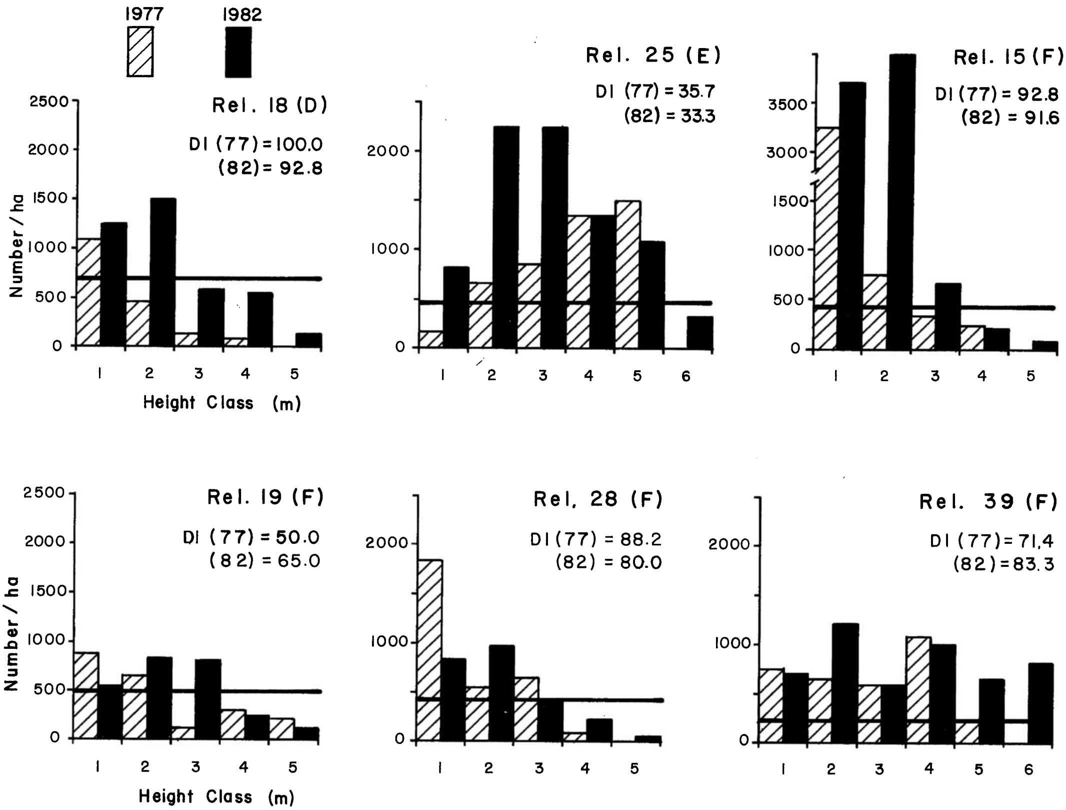

FIGURE 6. Frequency histogram of the number of saplings (0.5–5 m tall) per hectare for the different height classes recognized—"very advanced regeneration" group. The number of mature trees per hectare is indicated by the solid, horizontal line on each graph.

stand and the abundance of ʻōhiʻa saplings (Table 2). The notable exceptions to this association are the relative lack of saplings in relevé 20 and the two hot-spot dieback stands (relevés 13 and 37), and the apparent high level of regeneration in relevé 25, which had a maximum Dieback Index of 35.7%.

Relevé 20 represents a stand less than 200 years old (Holcomb 1980). Although it has a Dieback Index of 61.1% for 1977 and 66.6% for 1982, its sapling-to-tree ratio did not exceed 1.0. The establishment of ʻōhiʻa saplings in this stand is believed to be complicated by the presence of several invasive species of introduced plants in the understory, including *Andropogon virginicus* L. (Gramineae) and *Anemone hupehensis* (Lem. & Lem. f.) Lem. & Lem. f. (Ranunculaceae). We speculate that the introduced plants in this forest are in direct competition with ʻōhiʻa seedlings for both rooting positions and light, thus limiting the establishment of ʻōhiʻa saplings.

The small number of saplings in the two hot-spot stands (13 and 37) may, in part, relate to the size of the tree canopy affected by dieback. Although most of the trees in these two areas were killed, the total area of canopy defoliation was less than 900 m^2 in each stand. The small size of the canopy opening, in forests with trees over 20 m tall, may not allow enough additional light to reach the forest floor to foster the establishment of new saplings. A second factor has confounded this process in relevé 37. Although, by 1982, all the canopy trees in this stand were either dead or severely defoliated, the number of saplings per hectare decreased from what was recorded in 1977. However, since 1977, the subcanopy layer of tree ferns has increased considerably, effectively reducing the light available to ground-rooted saplings. In this regard, relevé 37 would perhaps be more appropriately grouped with the displacement dieback stands. It was classified as hot-spot dieback based on the small size of the area affected.

Relevé 25 shows the opposite situation: an extremely large ratio of saplings to trees for a stand with a low Dieback Index. This stand also represents a relatively small area that is distinctly different from the adjacent forest. In this case, the trees are fairly short in stature (10–12 m tall), with an open canopy and no tree fern layer. It is located in a small boggy depression and is surrounded by a taller forest, which is classified as severe wetland dieback (relevé 28). We suspect that the drastic reduction of the tree canopy in the adjacent forest also allowed more favorable conditions for sapling establishment in this otherwise nonaffected small stand.

We suggest that the four groups of frequency histograms for ʻōhiʻa saplings in each relevé (Figures 3–6) are related to both the occurrence of dieback in an area and time since the canopy trees were defoliated. The differences in the ʻōhiʻa population structure for stands in the early regeneration stage (Figure 4) through the advanced (Figure 5) and very advanced (Figure 6) regeneration stages are the result of an increased number of individuals in the taller height classes of saplings. If, as we have assumed, the height of a sapling is a true reflection of its age, this apparent wave regeneration trend is valid. Although we do not presently have sufficient age–size sapling data to verify this hypothesis, our observations generally agree with Burton's (1980) results, which showed a correlation between ʻōhiʻa seedling development and the amount of light reaching the forest floor. It would follow that the longer the time since the tree canopy cover was reduced, the taller the saplings would grow, graduating from the small height classes to the larger classes.

CONCLUSIONS

The concerns expressed regarding the fate of the Hawaiian ʻōhiʻa forests following intensive and widespread canopy dieback are well justified. A drastic change in both the vegetation structure and composition of this forest could have significant negative effects on both the watershed quality of the area and its value as a habitat for numerous species of endangered plants and animals.

Our results, plus Burton's (1980) work, indicate that the establishment of ʻōhiʻa seedlings and subsequent maturation of the saplings is strongly related to the degree of canopy opening and the amount of light reaching the forest floor. The high levels of regeneration found in most of the stands that had experienced a heavy to severe canopy dieback give us a fairly optimistic outlook that ʻōhiʻa will indeed be able to regain its canopy dominance within a relatively short period of time.

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